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Interspecific mycelial interactions – an overview

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The value of interaction studies

Two organisms may be said to interact when the presence of one in some way affects the performance of another. Such interactions are a salient feature of the fungal way of life, being an inevitable consequence of proximity or contact between individuals of the same or different species. They may occur quite simply because of common exploitation of a resource, or, as in the more complex example of mycoparasitism, because one organism serves directly as a nutrient source for another. Interspecific interactions in the former category are the particular concern of this chapter.

For organisms with a determinate body form, interspecific interactions are often regarded as becoming minimised by partitioning and specialism into separate niches. However, in mycelial fungi the indeterminate body form, combined with their versatility in requirements for growth and reproduction, increase the probability of interactions being both more obviously manifest and more frequent determinants of their distribution at any one time. Studies of interactions are therefore important if the development of natural fungal communities is to be understood. By the same token, they can also provide an understanding of the context within which the activities of fungi can be exploited in the biological control of pests and pathogens, under natural or semi-natural conditions. More fundamentally, studies of interaction patterns may help to provide an insight of processes involved in the functioning of mycelia and their capacity to co-ordinate their activities.

Approaches to interaction biology

Previous approaches

Interactions of fungi amongst themselves and with other types of organisms have long been studied, the diversity in approaches perhaps equalling the range of the interactions themselves. Attempts to clarify the interactions have, as with much of fungal ecology, been derived from ideas developed from other fields (Burkholder, 1952; Clark, 1954; Odum, 1954). This introduces the danger of applying concepts and principles appropriate for some organisms, but inappropriate for fungi. Further, confusion may arise if classifications of interactions between fundamentally different groups of organisms (as occurs for example, in the formation of mycorrhizas and leguminous root nodules) are applied to closely similar organisms. Another difficulty arises from the emphasis which has been traditionally placed upon soil fungi, which may have distorted the development of principles, overemphasising some facets, whilst underemphasising others.

In an early attempt at synthesis, Park (1960) described harmless or beneficial associations as symbiosis, but those detrimental to at least one of the interacting fungal partners as antagonistic (Fig. 1). Since then, it has become widely accepted that the mechanisms of antagonistic action include antibiosis, parasitism and competition – the latter usually involving rivalry for nutrients and growth factors, rarely for space and oxygen (Park, 1960, 1968; Clark, 1965; Baker & Cook, 1974). Whilst the boundaries between these three forms of antagonism were recog-

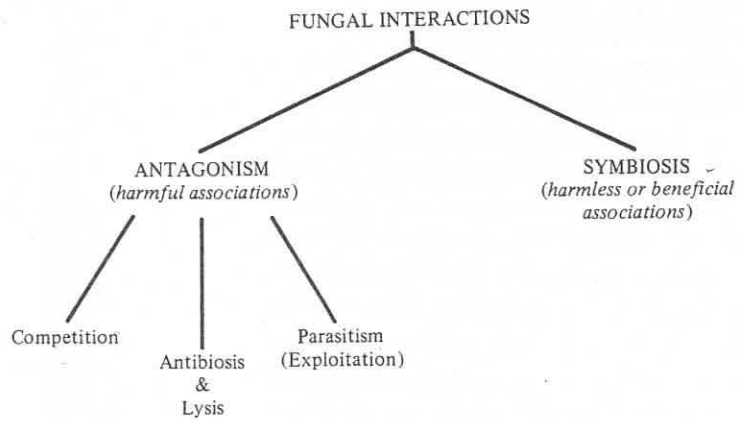

Fig. 1. Previous schema of fungal interactions. (After Park, 1960, 1968; Clark, 1965; Baker & Cook, 1974.)

nised to be indistinct, this has not prevented sometimes protracted debate concerning which mechanism is the most widespread or important. Early work on fungistasis in soils (Dobbs & Hinson, 1953; Dobbs, Hinson & Bywater, 1960) suggested to many that non-specific antibiosis was the primary form of antagonistic action. Characterisation of specific antibiotic substances, and the pairing of fungal isolates in culture, which often demonstrated inhibition in growth of one 'target' organism (mutual inhibition perhaps being often overlooked), tended to reinforce this concept (Brian, 1957).

However, the primary division shown in Fig. 1 into antagonism and symbiosis, whilst arguably applicable to interactions between dissimilar groups of organisms, is not a particularly helpful dichotomy when applied to mycelial interactions. It is difficult to reconcile the few known examples of harmless or beneficial associations between fungi with the widely accepted view of symbiosis as a persistent intimate association between individuals. In addition, a return to the original view of de Bary (1887) that all such persistent, intimate associations are symbioses regardless of their harmful, harmless or beneficial consequences (Lewis, 1973; Cooke, 1977), make present use of the term symbiosis ambiguous.

The subdivision of antagonism into three mechanisms may also confuse. Firstly, the term competition is used only in a narrow sense, out of keeping with the broader concepts of general ecology and evolution, and subservient in hierarchical terms to antagonism. The paradox is apparent in the exclusion from the scheme of Garrett's important concept of *competitive saprophytic ability*, because it encompases both competition for nutrients and antibiosis (Garrett, 1956, 1970). Secondly, whilst antibiosis has tended to be given prominence, other mechanisms, such as hyphal interference, have not been incorporated into the scheme. As already suggested this may be a legacy of the early emphasis on soil fungi. Soil being an open, heterogeneous, finely divided, spore-filled environment, observation of any active fungal mycelia within this system must be difficult. Consequently, experimental approaches to investigating interactions in soil have of necessity often been *in vitro*. As many soil fungi are typically those which produce abundant spores which germinate and grow rapidly on culture plates, notably many Fungi Imperfecti, these and their interactions will be given prominence.

A final and perhaps most important difficulty with a terminology based solely on consideration of mechanism rather than the outcome of interactions creates difficulty is that it introduces the constraint that

before classification can be made, mechanism has to be decided upon, often without appropriate data to hand. Directly observable outcomes of interactions therefore provide a much more flexible basis for classification, particularly since a single outcome may result from a combination of mechanisms.

Garrett placed outcome before mechanism in his approach to interaction studies, when considering competitive saprophytic ability. Experimentally, this involved the exposure of an uncolonised resource (such as an agar plate, a wheat straw) to a mixed microbial inoculum (usually in soil) and analysis of the resultant colonisation patterns. Organisms achieving dominance in the early stages of colonisation were regarded as possessing high competitive ability, and only secondarily were the mechanisms of their success considered. However, consideration of what might follow once a resource had become fully occupied was omitted. Interaction outcomes during both early and late phases of colonisation were subsequently recognised by Gibbs & Smith (1978) and termed 'primary' and 'secondary' antagonism respectively. For reasons which will become apparent, this categorisation may be misleading when used in a general context, since it implies that events occurring during primary colonisation should necessarily be interpreted as 'antagonism'.

More recently, an attempt has been made to apply the concepts of *exploitation competition* and *interference competition* to fungi, these terms having initially been developed for other organisms (Lockwood, 1981; Wicklow, 1981*a*). Exploitation competition is restricted to the depletion of resources by one organism, or population, without reducing the access of another organism, or population, to the same resource pool. Interference competition involves behavioural or chemical mechanisms by which access to a resource is influenced by the presence of a competitor (McNaughton & Wolf, 1973). But the application of these terms to mycelial fungi is both inadvisable and misleading (Cooke & Rayner, 1984). During resource depletion many, and possibly most, mycelial fungi do restrict access of others, either by efficient nutrient uptake or through dense branching hyphal systems or other mechanisms (see below). Thus the term exploitation competition divorces competition for nutrients from a consideration of the space in which they are contained. The outcome of using the term is the conclusion that competition for nutrients is of prime importance, that for space being negligible (Lockwood, 1981). Whilst correct within context, the conclusion can be misleading since with most mycelial fungi occupation of space is inseparably linked with the utilisation of resources.

In view of these varied approaches and mixed philosophies we believe there is a need for a rationalisation of outlook commensurate with the mycelial way of life, that also takes account of the full range of fungal activities in natural habitats. A first step towards this is to examine how the types of interaction are related to the life strategies of mycelial fungi.

Interactions and life strategies

As will be apparent from other contributions to this Symposium, the fungal mycelium in its natural habitat is a heterogeneous complex, dynamic entity in which phases of establishment, exploration and exploitation of resources and reproduction occur in overlapping sequence. The timing and duration of these phases crucially affects the interactive properties of a mycelium and hence its role in population and community development.

Thus in some fungal species, rapid germination and extension growth are associated with essentially explorative mycelium, utilising only readily assimilable substrates with early commitment to reproduction. In other cases, the exploitative phase is prolonged, involving utilisation of more refractory substrates and delayed commitment to reproduction. These alternatives are the extremes of the spectrum between *r*- and *K*-selection in which organisms are visualised as being fitted either for an ephemeral or sustained existence respectively (e.g. MacArthur & Wilson, 1967; Harper & Ogden, 1970; Andrews & Rouse, 1982). Whilst an ephemeral existence obviates the requirement for maintenance of activity in the presence of other organisms, a sustained existence demands either the ability to withstand (or even exploit) the presence of other organisms or of conditions (stress) which militate against their survival. These considerations have led Grime (1979) to suggest for higher plants that three major ecological strategies exist: ruderal, competitive and stress-tolerant, and these same strategies can also be applied to fungi (Pugh, 1980). Using the term combative rather than competitive, the former being perhaps more appropriate to fungi, Cooke & Rayner (1984) have then attempted to rationalise the diversity of fungal activities within these three primary strategies.

Proposed schema

Following the above, mycelial interactions are described on the basis of proposals made by Cooke & Rayner (1984) and illustrated in Fig. 2. The primary division is into competitive, neutralistic and mutualistic interactions between two participants, depending

respectively upon whether the outcome is detrimental to either or both, detrimental to neither but not beneficial to both, or beneficial to both.

One feature of the schema is that the hierachical position of competition and antagonism is reversed from that in Fig. 1, competition being used in its more usual broad sense, and antagonism more specifically as the mechanism underlying a particular type of competition (i.e. combat). We have followed the simple definition of competition between organisms, namely that of an active demand by two or more individuals of the same or different species for the same resource. Following from the earlier discussion of exploitation and interference competition and primary and secondary antagonism it is evident that during colonisation of an initially vacant resource, two basically different aspects of competition must be distinguished, which are termed primary resource capture and combat.

Primary resource capture describes the process of gaining initial access to, and influence over, an available resource. It is an apt term for mycelial fungi in which the indeterminate thallus facilitates potentially continuous expansion of territory. Since primary resource capture is dependent solely on priority of arrival and sequestration of resources before the occupied domains become contiguous, it does not involve direct challenge between individuals in close proximity except perhaps during initial establishment at the surface of the resource. Success in

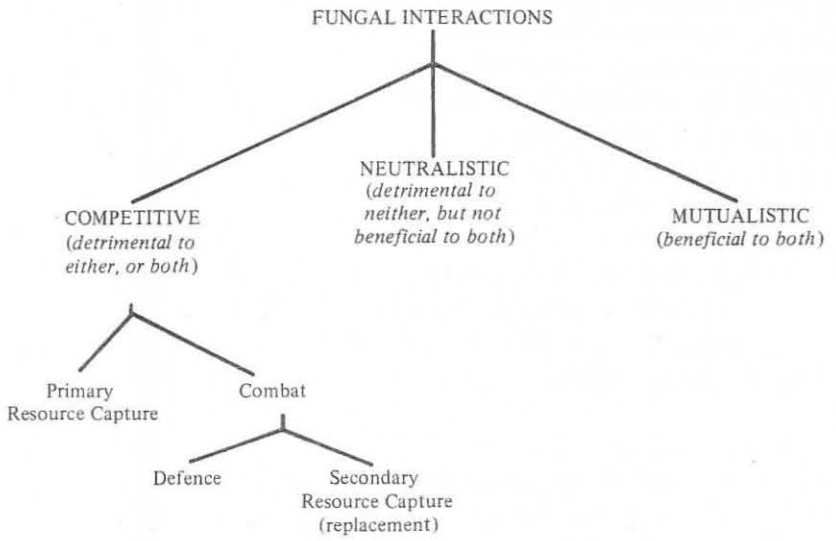

Fig. 2. Proposed schema of fungal interactions. (After Cooke & Rayner, 1984.)

primary resource capture is therefore determined by such factors as effective dispersal mechanisms, spore germination, mycelial extension rates, possession of suitable enzymes to utilise available substrates, and tolerance of adverse conditions (stress) associated with the resource. Thus fungi with at least partially ruderal strategies are favoured in primary capture of resources relatively free from stress by powers of early arrival and rapid exploration, whilst stress-tolerant fungi are favoured by being adapted to physicochemical or nutritional stress associated with the resource.

As primary resource capture proceeds so the domains of different individuals increasingly come into contact. When this happens three events may follow. There may be unilateral or bilateral intermingling via neutralistic or mutualistic interactions (see below), mutual exclusion, or replacement of one individual by another. The latter two events may under some circumstances result from purely nutritional factors; thus effective uptake of nutrients by one individual may be sufficient to deny another individual access to its domain. Alternatively, one individual which has exhausted supplies of nutrients which are assimilable to it may then be replaced by another individual capable of utilising the residue. However, mutual exclusion and replacement also occur as a result of more direct physiological challenge between individuals such that access to one individual's domain may be prevented by active defence, or achieved via active secondary resource capture mechanisms. This is described as combat, and those fungi which exhibit it as combative, or as having a combative ecological strategy. Collectively the mechanisms underlying combat are encompassed by the term antagonism. Of course the combative ability of a fungus is determined partly by its physiological state, so that changes in physicochemical or nutritional conditions associated with resource utilisation will affect the outcome of interaction between two combatants.

As has been implied, defence and secondary resource capture represent two different aspects of combat. In defence, access to resources gained by primary capture is denied to another individual. Hence success of a fungus able principally in defence will rest on its ability for effective primary capture. In secondary resource capture, access is gained to an already occupied domain, so that fungi able in this aspect of combat need not necessarily be effective in primary resource capture.

Although emphasis is normally placed on the competitive interactions just described, there are two obvious ways in which fungi may associate non-competitively in nature, via neutralism and mutualism.

There are two possible kinds of neutralistic associations between fungi. In the first, association results in no discernible benefit or harm to the associated species, interaction being either absent or so minor as to produce no detectable effects. This type of essentially passive co-existence, though it seems to be common between fungi and bacteria, is probably rare between fungi. In the second kind of neutralistic association, one of the associates benefits in some way from the activities of the other without conferring any benefit or harm in return.

Mutualistic associations are those in which each associate benefits from the activities of the other. In view of the wide range of habitats open to fungi, and the great variety of fungi commonly found within them, it is possible that mutualism and the second kind of neutralistic interaction commonly occur by chance. However, as will become apparent, too few examples are presently available to assess the extent and significance of neutralism and mutualism and their physiological bases.

Interactions in culture

Neutralistic and mutualistic interactions

The most direct initial evidence for a neutralistic or mutualistic interaction in culture is intermingling of mycelia. However, it must be noted that intermingling may be facilitated in sparse mycelial systems because interdigitating hyphal branches are allowed access to uncolonised substratum. Hence the nutritional conditions must be taken into account before a decision is made to the effect that a particular combination of individuals show an intermingling response. Low nutrient availability may allow apparent intermingling between correspondingly sparse mycelial systems, which under conditions of higher nutrient concentrations might be mutually exclusive. Here, intermingling at low concentrations is really due to continued exploration and primary resource capture. By the same token, it must be accepted that intermingling mycelia may still be depleting resources from the same resource pool and hence be in competition (cf. earlier mention of exploitation competition). For the association to be truly neutralistic different portions of the resource pool should be utilised. One way in which this could be achieved in culture is where 'staled' parts of a colony of one individual become occupied by another. Similarly, some fungi may survive on waste products or exudates from hyphae of another, especially if the latter are autolysing. *Penicillium* and *Cladosporium* contaminants of basidiomycete cultures probably behave in this way.

Under conditions which favour dense mycelial growth, intermingling between mycelia appears an exceptional event. However, fungi which have constitutively sparse, explorative mycelia such as certain coenocytic Mucorales, may invade domain already occupied by another fungus without necessarily deleteriously affecting the latter. In a study of the interactions of the Dutch Elm disease pathogen, *Ceratocystis ulmi*, with a wide range of bark-inhabiting fungi, only two instances of an apparent intermingling reaction were recognised, namely with *Cladosporium herbarum* and *Graphium penicillioides* (Webber, 1979; Fig. 3). Here, intermingling was manifested by stimulated production of synnemata of *C. ulmi* within the colonies of *C. herbarum* or *G. penicillioides*. Axenic cultures of *C. ulmi* normally lack synnemata.

Stimulation of sporulation has been very widely reported as a consequence of mycelial interactions, and represents one way in which an individual may benefit without necessarily bringing about deleterious effects in the other. It may therefore be regarded as one basis for neutralism and for mutualism. However, it is more likely that stimulation of the reproductive mode results from deleterious action on the vegetative mode, and that any advantage accrued must be viewed against the basic life strategy and energetics of the fungus concerned.

One example of the type of interaction just described is provided by what has been termed the '*Trichoderma* effect', observed amongst many heterothallic species of *Phytophthora*. The effect is confined to the *A2* compatibility type and, perhaps significantly, is especially marked amongst species invading roots of woody hosts, such as *P. cinnamomi, P. cambivora* and *P. palmivora*, where contact with *Trichoderma* species is likely to occur (Brasier, 1975*a,b*, 1978). The effect involves stimulation of the production of oospores via self-fertilisation in mycelial cultures exposed to volatile antibiotics from *Trichoderma* strains, variability between *Trichoderma* strains in eliciting the effect being correlated with their production of antibiotics. Since the effect is due to antibiotics, it is evident that it may at least partially function via deleterious effects on the vegetative phase, and indeed *Trichoderma* eventually replaces the *Phytophthora* species. However, the deleterious effect of replacement might be viewed as being counteracted partly by the production of survival structures (the oospores), but also by the stimulation of sexual reproduction in the absence of the *A1* compatibility type. Typically there seems to be a marked imbalance between the compatibility types in *Phytophthora* populations, for example amongst a world-wide sample of *P. cinnamomi* isolates, 28 were *A1* and 632 *A2*.

Such an imbalance may be seen either as leading to a requirement for, or being a consequence of, the *Trichoderma* effect.

Another example of a change of mode brought about by interactions occurs in stimulation of rhizomorph and mycelial cord formation. Thus rhizomorph development in *Armillaria* is stimulated by the presence of

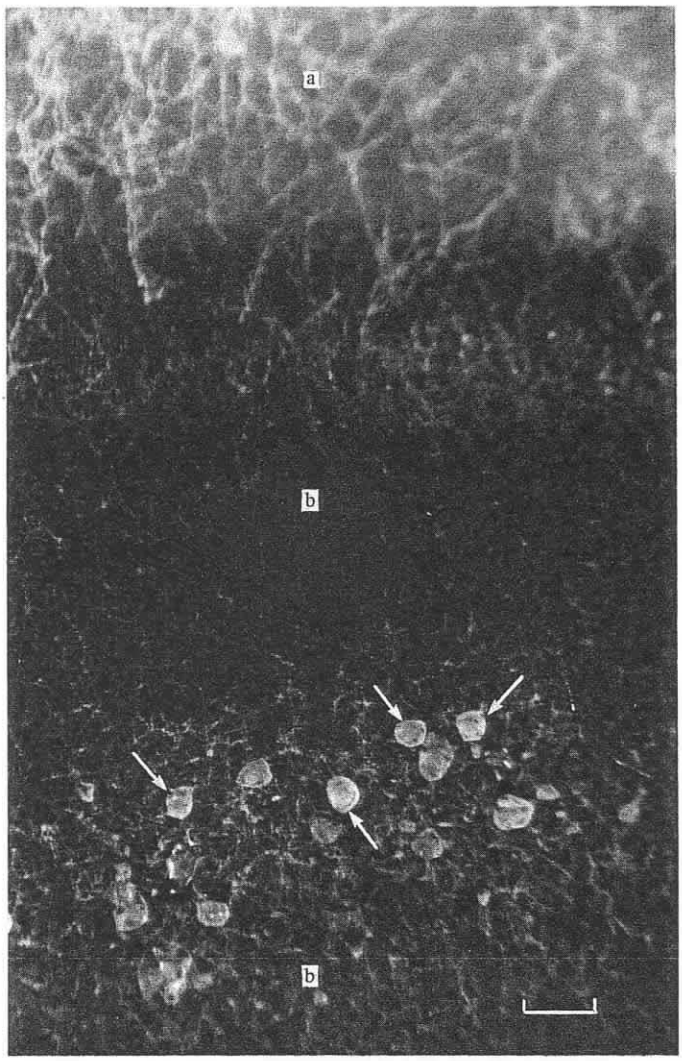

Fig. 3. Intermingling reaction between *Ceratocystis ulmi* (a) and *Cladosporium herbarum* (b) on 2% malt agar. The heads of the synnemata (arrowed) produced by *C. ulmi* are clearly visible within the *C. herbarum* colony. Scale bar, 2 mm.

Aureobasidium pullulans, apparently via ethanol production (Pentland, 1965, 1967) and in *Sphaerostilbe repens* it is stimulated by a number of fungi including *Penicillium thomii, Aspergillus niger* and *A. amstelodami* (Botton & El-Khouri, 1978). Mycelial cords of fungi such as *Phallus impudicus* and *Phanerochaete velutina* appear to be induced to form at a distance by *Penicillium* species and then may show directed growth towards the latter (L. Boddy & A. D. M. Rayner unpublished; Fig. 4). As is indicated by Thompson (Chapter 9) mycelial cord formation in several Basidiomycotina is favoured by growth under non-sterile conditions.

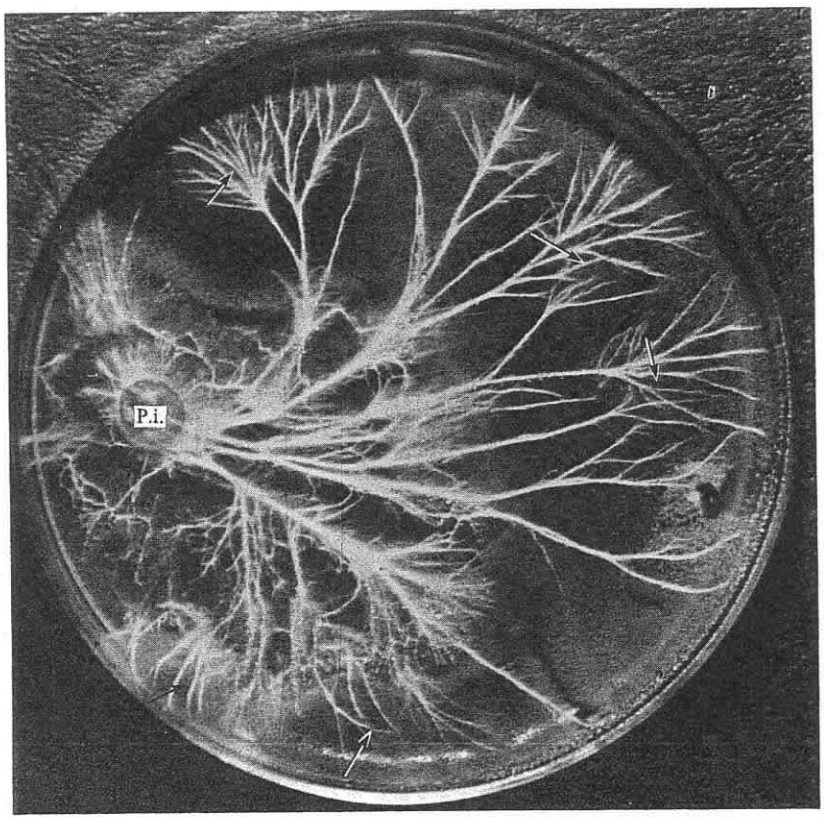

Fig. 4. Interaction between *Phallus impudicus* (P.i.) inoculated on one side of a 2% malt agar plate, and a series of colonies of *Penicillium* (the positions of the centres of some of which are arrowed) which developed around the periphery of the plate. Cords of *P. impudicus* have grown towards the *Penicillium* colonies prior to fanning out across them. (Photograph by Mr S. J. Payne.)

Neutralistic interactions may occur when readily assimilable substrates released by extracellular enzyme action of one fungus on a more complex and hence refractory substrate, are made available to another, associated species, not itself capable of breaking down the more refractory substrate. Thus *Melanospora destruens,* unable to use inulin, has been reported to grow well on a medium containing no other carbon source in mixed culture with fungi which can break down this substrate. Similarly, it grows more luxuriantly on sucrose-containing media in combination with fungi with greater powers of inversion (Hawker, 1947). Garrett had this situation in mind when he postulated the occurrence of so-called 'secondary sugar fungi' associating with cellulolytic and lignolytic species in decomposing plant residues. Whilst the existence of such fungi has been widely assumed (Hudson, 1968) there is little direct evidence for it. Tribe (1966) suggested that *Pythium oligandrum* associating with *Botryotrichum piluliferum* and *Fusarium* species on cellulose films was behaving as a secondary sugar fungus, but subsequent studies indicated that it may be in fact behaving as a mycoparasite (Deacon, 1976). Hedger & Hudson (1974) obtained evidence that *Thermomyces lanuginosus* growing in association with *Chaetomium thermophile* on filter-paper cellulose or wheat straw benefited from reducing sugars released by the cellulolytic activity of the latter fungus. Whilst mycoparasitism of *C. thermophile* cannot be ruled out they found no direct evidence for it.

It has been pointed out that removal of reducing sugars by an associated sugar fungus may limit catabolite repression, and hence enhance cellulase production by a cellulolytic fungus (Hulme & Stranks, 1970). Also since cellulase is an enzyme complex, mixtures of cellulases from different fungi growing together may be more efficient than those of any individual (Wood, 1969; Hulme & Shields, 1975). Whilst these examples illustrate synergism in cellulose breakdown, they should not automatically be regarded as mutualistic associations; enhanced cellulose breakdown may not necessarily be in keeping with the particular strategies of the participants. Nevertheless, such examples do illustrate how complementary physiological activities can provide a basis for mutualism.

Complementarity can also be found in culture by growing fungi on media lacking vital growth substances. Thus *Nematospora gossypii* and *Bjerkandera adusta* can grow in mixed culture on a synthetic medium lacking biotin, inositol and thiamin, but not individually. Whilst *B. adusta* can synthesise biotin and inositol, it cannot synthesise thiamin.

N. gossypii can synthesise thiamin, but not biotin and inositol (Kogl & Fries, 1937).

Competitive interactions

It is seldom possible to predict from cultural experiments the effectiveness of a fungus in primary resource capture, since this is frequently associated with a specificity to the resource which can never be reproduced under cultural conditions. Studies of mycelial extension rates and enzymic capacity can provide some indirect measure of ability in primary resource capture, but these methods may have questionable relevance under field conditions. Therefore, studies of competitive interactions in culture have usually concentrated on the outcome of combative confrontation between mycelia (usually two paired opposite one another on agar medium) rather than to the preliminary events of resource capture as the colonies become established. Where sufficient nutrients are available to allow dense mycelial development two outcomes of confrontation between mycelia are usually observed: deadlock in which neither individual invades territory occupied by the other, and partial or total replacement, in which one individual destructively invades another's territory. Whilst as indicated previously, these outcomes may sometimes result from purely nutritional factors, in others they result from direct physiological challenge (combat/antagonism).

Interactions of the latter type may be classified in terms of their underlying mechanisms (Fig. 5). Two main types are recognised. These are firstly, interactions which are mediated at a distance through diffusible or volatile substances (antibiotics) which result in inhibition or

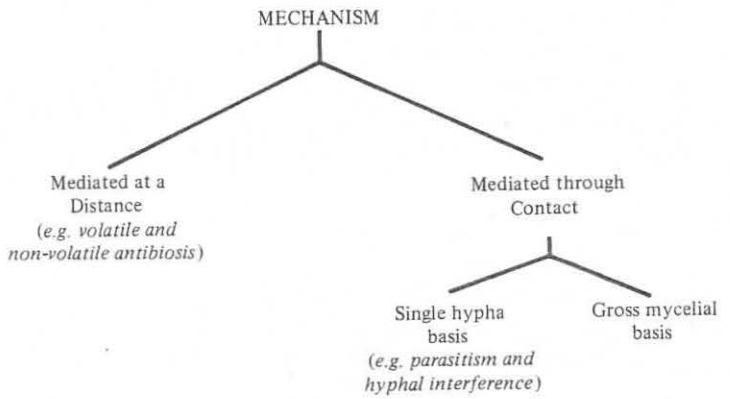

Fig. 5. Mechanisms of combat.

cessation of growth of one or both mycelia. Unilateral inhibition may be a prelude to replacement, whilst bilateral inhibition inevitably results in deadlock. The second type of interaction occurs only following contact, and may again result in deadlock or replacement. Contact between individuals, with its consequent varied outcome, may be effected either at the level of individual hyphae, as in hyphal interference and necrotrophic mycoparasitism, or by gross contact between mycelial systems.

There appears to be some correlation between the types of interaction in which a fungus becomes involved and its mycelial organisation and life strategy. As a generalisation, fungi with coenocytic, rapidly extending mycelia tend not to have antagonistic properties; septate Ascomycotina, Deuteromycotina and Mucorales (*Mortierella* species) often operate antagonistically via antibiosis; whilst Basidiomycotina usually operate via contact antagonism. That some of these differences in interactive properties are based on functional qualities associated with mycelial organisation, and that this transcends taxonomic divisions, is emphasised by the behaviour of certain Basidiomycotina. *Phlebia radiata* and *Phlebia rufa* exhibit what is known as astatocoenocytic behaviour (Boidin, 1971) and both primary and secondary mycelia develop behind a rapidly extending broad front of appressed coenocytic hyphae. This front is followed by septate mycelium, with extensive aerial proliferation and, in secondary mycelia, clamp-connections (Boddy & Rayner, 1983*a*; Fig. 6). The coenocytic front is non-combative, and is readily replaced by many fungi paired against it. However, once contact with septate mycelium of the *Phlebia* species is established this typically develops a dense zone of aerial mycelium, which advances across opposed mycelia via successive waves of lysis (Fig. 7*a*). It is as though exploration, consolidation and combat are mediated through morphologically diverse mycelial stages in these fungi. Less obvious but similar transitions probably occur in many fungi, and may greatly influence the dynamics of their interaction responses.

Mechanisms of combat (antagonism)

Antibiosis. The historical accident of the discovery of penicillin, together with the striking appearance of colony inhibition at a distance, have probably combined to make antibiosis in its broadest sense the most frequently reported phenomenon between fungi interacting in culture. Whilst long-range inhibition may be brought about by a wide variety of mechanisms, including the production and accumulation of

general waste products, changes in pH etc., the accent has usually been on single volatile or diffusible substances produced by particular strains of fungi. This accent follows from the attempts to discover practically useful antibiotics, and their efficacy towards particular 'target' organisms considered for one reason or another as pests. There is no doubt that this approach has been useful in leading to the isolation and characterisation of particular antibiotic substances. Included amongst these is griseofulvin, isolated originally by Brian, Curtis & Hemming (1946) from *Penicillium janczewskyi* and described as a 'curling factor' because of its effect on germ tubes of *Botrytis allii* and other fungi with chitin walls.

Successful as the search for antibiotics may have been (see also Moss: Chapter 6), it has provided only limited insight into their role in the dynamics of mycelial interactions themselves, perhaps due to the

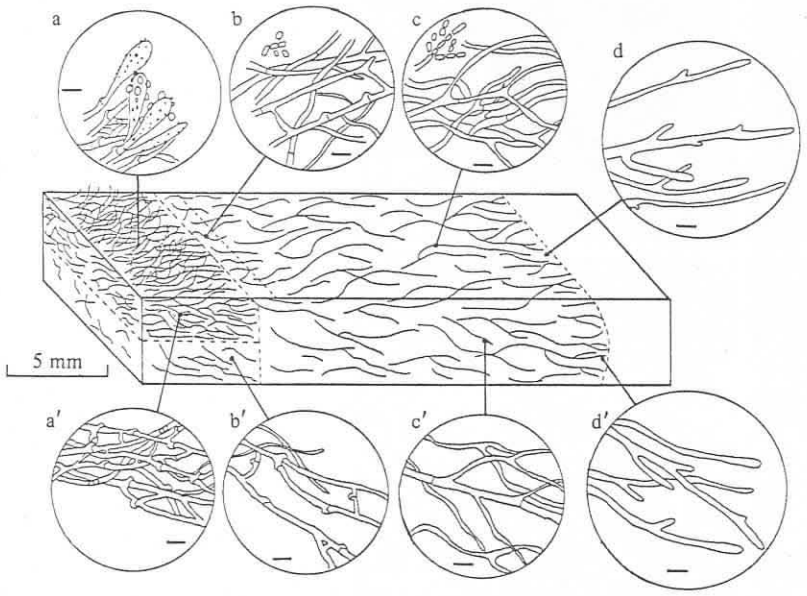

Fig. 6. Colony characteristics of a dikaryotic culture of *Phlebia radiata* growing through malt agar. Direction of growth left to right; a–d, surface mycelium; a′–d′, submerged mycelium; scale bar, 10 μm. a, hyphae with clamp-connections and cystidioles; b, heterogeneous mycelium with septa, anastomoses, pseudoclamps and oidia; c, heterogeneous mycelium, mostly coenocytic with oidia; d, wide coenocytic marginal hyphae. a′, closely packed mycelium with anastomoses and clamp-connections; b′, as in a′ but loosely packed; c′, heterogeneous mycelium, mostly coenocytic; d′, wide, coenocytic marginal hyphae. (After Boddy & Rayner, 1983*b*.)

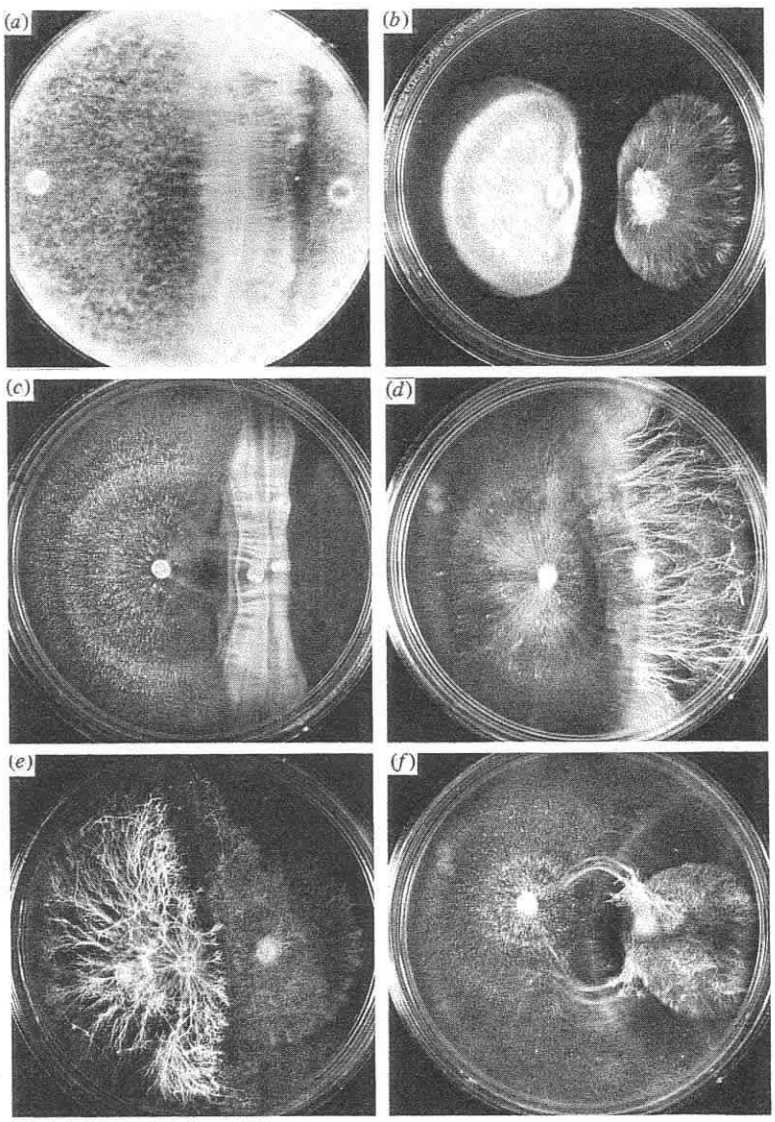

Fig. 7. Combative interactions involving various wood- and litter-inhabiting Basidiomycotina on malt agar. (a) *Phlebia radiata* (left) versus *Bjerkandera adusta*. Successive fronts of *P. radiata* are in the process of replacing *B. adusta* preceded by lysis of the latter. (b) Mutual inhibition at a distance between *Collybia confluens* (left) and *Clitocybe flaccida*. (c) Replacement of *Collybia butyracea* (right) by a dense mycelial front of *Collybia peronata*. (d) Replacement of *Clitocybe nebularis* (right) by *Collybia peronata*, with the normally appressed mycelium of the latter producing cords. (e) Replacement of *Clitocybe*

overemphasis of unilateral effects on a particular target organism, and on single chemical substances. Thus mutual inhibition, which is an extremely common feature of antibiotic interactions, has received little attention. In addition, the fact that a particular isolate may show antibiotic action only against certain fungi but not others, has been interpreted in relation to variation in sensitivity to the antibiotic, rather than differences in elicitation of its production.

These features of mutual inhibition, and apparent specificity of action, however, imply a more complex situation, possibly involving a reciprocal exchange of chemical signals between participants. For example, amongst certain litter-decomposing Agaricales, *Collybia confluens* and *Clitocybe flaccida* show a strong mutual inhibition when paired against each other in culture on 3% malt agar but are not inhibited in pairings against certain other species (Fig. 7*b*). They must therefore be responding in a very specific manner to each others' metabolic products, of which at least two specific substances must be involved. This type of situation suggests that some 'antibiotic' reactions involve a process of reciprocal exchange of chemical signals and recognition at a distance.

Hyphal contact. Whilst antibiosis was long regarded as the principle mechanism underlying many interactions, it has become clear that growth inhibition may often not occur prior to actual contact between hyphae or mycelia. One important mechanism resulting in contact inhibition has been termed hyphal interference (Ikediugwu, Dennis & Webster, 1970). This characteristically involves mutual or unilateral death of hyphae, or hyphal compartments as a result of intimate contact with one another. The death of cytoplasm in contacted compartments follows changes in membrane permeability, increased refractivity, vacuolation and eventual lysis. The process between *Coprinus heptemerus* and *Ascobolus crenulatus, Heterobasidion annosum* and *Phlebia gigantea* has been studied with the electron microscope. (Ikediugwu, 1976*a,b*). The affected compartments show a variety of abnormal

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Caption for Fig. 7 (*cont.*)

flaccida (right) by *Collybia dryophila*, with the normal cord-forming growth of the latter reverting to a diffuse, appressed mycelium. (f) Replacement of *Clitocybe flaccida* (right) by cords of *Collybia peronata* with the morphogenetic stimulus associated with cord-formation being transmitted far back into the colony of the latter. (Photographs b–f by A. G. Mitchell, from Cooke & Rayner, 1984.)

features. They contain lipid globules, vesicles of various types, and organelles such as mitochondria and nuclei become swollen. The swollen mitochondria subsequently become vacuolate as eventually does the whole cell. At the point of contact with the antagonising hypha a characteristic extraplasmalemmal zone develops with various types of vesicles radiating from it.

Hyphal interference appears to be a particular feature of higher fungi, especially Basidiomycotina. It also appears to involve a form of surface recognition and the process shows some similarities with hyphal fusion which has aborted at an early stage of development. Somatic incompatibility within many Basidiomycotina is typically expressed as a post-fusion event at the intra-specific level, the interval between fusion and lysis varying with different species. Very closely related species, such as *Phlebia radiata* and *Phlebia rufa* appear to exhibit fusion followed by virtually immediate lysis (Boddy & Rayner, 1983*a*), whilst *Stereum rameale* and *Stereum rugosum* produce very marked hyphal interference (Rayner & Turton, 1982). A connection between the ability for hyphal fusion and hyphal interference might help to explain the apparent predominance of the latter in the Basidiomycotina. Interestingly, the advancing non-combative coenocytic phase of *Phlebia* species totally lacks hyphal fusions (Boddy & Rayner, 1983*a*).

It may be only a relatively short step from hyphal interference to the point at which a hypha of one fungus, having killed that of another, is able to derive nutrients from it. The latter is probably always associated with the destructive action of *Gliocladium roseum*, which can attack a wide range of host species (Barnett & Lilly, 1962). However, parasitism may also be related to secondary capture of the resource in which the parasitised fungus is growing, as for example in the apparent parasitism observed in *Pseudotrametes gibbosa* and *Bjerkandera adusta* (Fig. 8). Both cause white rot of deciduous wood, but *P. gibbosa* selectively colonizes wood previously occupied by *Bjerkandera adusta* (Rayner, 1978; Rayner & Todd, 1979).

The possible close connection between hyphal fusion, hyphal interference and parasitism is further suggested by observations of coiling reactions in di-mon mating of *Schizophyllum commune* (Nguyen & Niederpruem: Chapter 4). Such coiling is a characteristic feature of necrotrophic parasites, but biotrophic parasites which often obtain their nutrients from living cells may show a wide range of intercellular reactions (Barnett & Binder, 1973). That Buller should have regarded parasitic fusions as being a third kind of hyphal fusion (Gregory:

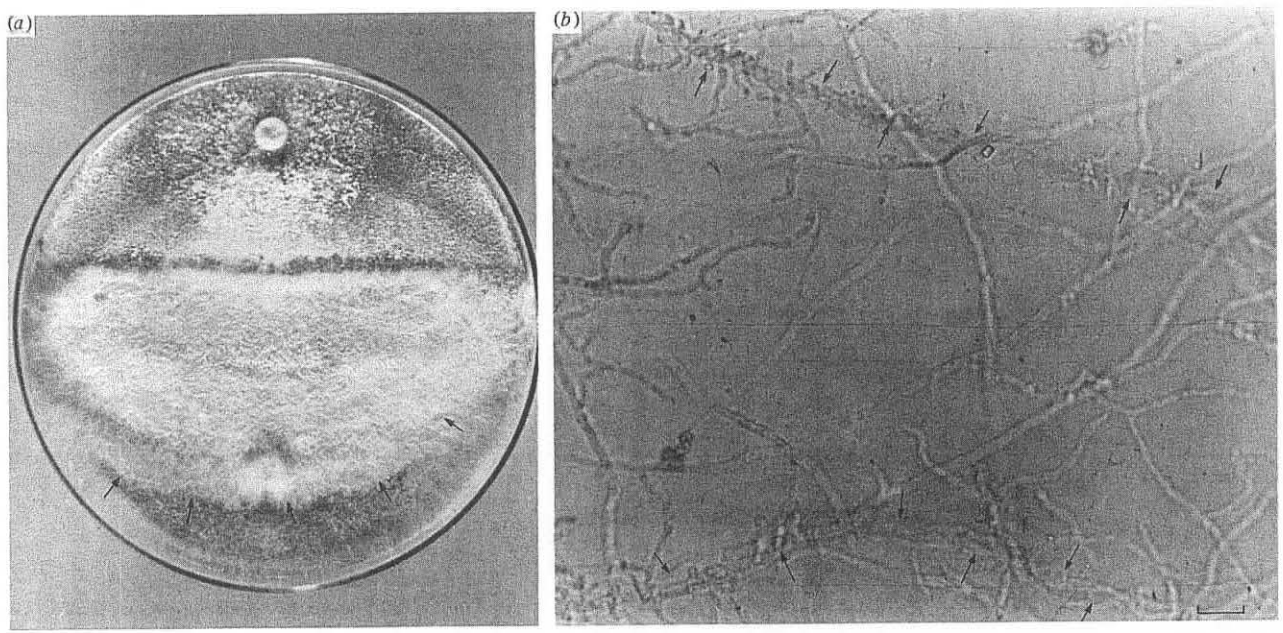

Fig. 8. Necrotrophic mycoparasitism of *Bjerkandera adusta* by *Pseudotrametes gibbosa*. (a) Interaction on 3% malt agar showing replacement by a dense mycelial front (arrowed) of *P. gibbosa*. (After Rayner & Todd, 1979.) (b) Aggregation of branches of *P. gibbosa* around two dead hyphae of *B. adusta* (arrowed). Scale bar, 10 μm.

Chapter 1) might have significance here. However, biotrophic mycoparasitism does not lead to secondary resource capture – the parasitised fungus is the resource, and is therefore beyond the scope of this discussion.

Mycelial contact. Observation of basidiomycete interactions in particular, suggest that mechanisms involving gross mycelial contact between colonies are important determinants of deadlock and replacement. Very often a dense zone of mycelium is produced at the interaction interface; this may be mutual in deadlock, or unilateral in replacement interactions where a dense wave of mycelium progressively advances across the opposing colony, often preceeded by lysis (Fig. 7c). Similarly, aggregated structures, such as cords, are often differentiated prior to replacement. Although such replacement may be brought about by lysis and parasitism on a huge scale, the underlying mechanisms of such gross interactions are still largely unknown. In some cases it may be that they simply have a 'smothering' effect on the mycelium replaced. Nonetheless, the specificity with which such interactions occur in different combinations, together with the elicitation of dense mycelium, suggest that some form of recognition response is involved.

Mycelial co-ordination during interactions. Combative interactions with another mycelium are likely to test the powers of co-ordination of mycelial activities, including effectiveness of mobilising resources from a non-interacting region to a site of confrontation. This feature is particularly evident amongst Basidiomycotina many of which exhibit marked combative ecological strategies. Little work has been done in this connection, but it certainly provides a potentially useful approach to studying the physiological functioning of mycelia.

Evidence for such co-ordination of activities and the dynamic nature of combative interactions is seen in Fig. 7 d–f, where for example 'lines of communication' to an interacting front of mycelial cords is evident (Fig. 7f). Similarly, a mycelium which is actively replacing another (for example *Pseudotrametes gibbosa* replacing *Bjerkandera adusta*) often remains relatively sparse behind the replacement front as compared with control plates or some deadlock interactions (Fig. 8).

The dynamic equilibrium behind two combative mycelial fronts is sometimes evident when bi-directional replacement occurs. This is commonly seen in interactions between *Piptoporus betulinus* and *Phlebia radiata* for example, where replacement occurs through 'access'

points or 'bridgeheads' in the interaction fronts (Fig. 9a). With *P. radiata* and *Coriolus versicolor* the normal interaction, following replacement of the coenocytic phase of *P. radiata*, is a deadlock between vigorous interaction fronts. However if a strip inoculum of *P. radiata* subcultured from an established mycelium is placed against *C. versicolor* the balance of power is changed, so that lysis of *C. versicolor* occurs opposite the strip inoculum, whilst replacement of explorative *P. radiata* mycelium occurs at the edges of the interaction front (Fig. 9b).

Interactions in natural substrata

Problems of identification

The great value of cultural studies of interactions is their convenience and the fact that underlying mechanisms can often be ascertained simply by observation. However, doubt always exists concerning the relevance of such interactions under natural conditions, and so an attempt must be made to ascertain what events may be occurring under these conditions. These attempts usually start with the use of 'semi-natural' substrata, under laboratory conditions, and culminate in the study of the dynamics of truly natural communities. An important feature is that whilst intermingling, replacement and deadlock interactions

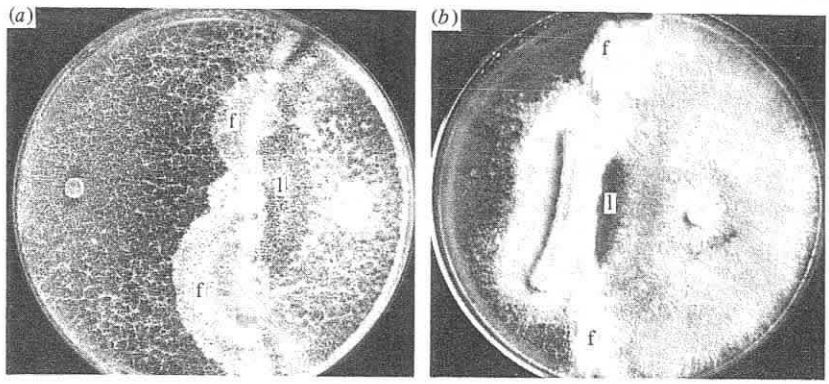

Fig. 9. Bi-directional replacement interactions on malt agar involving *Phlebia radiata* (left) versus: (a) *Piptoporus betulinus*, which has produced dense fan-like fronts through gaps in the *P. radiata* reaction front, but has undergone lysis elsewhere; (b) *Coriolus versicolor* – here a strip inoculum from established mycelium of *P. radiata* has been used. *C. versicolor* has undergone lysis immediately opposite the strip, but has formed replacement fronts over the sparse mycelium on either side of it. (Photograph by Nicola Kemp.) l, lysis; f, replacement fronts.

may be observed in natural substrata; interaction mechanisms must remain obscure unless supported by cultural work.

Because of the many difficulties inherent in studying interactions in the field, much of the evidence for them is indirect, based on the studies of succession on decomposing substrata. Unfortunately, interpretation of interactions in this way has been clouded by a lack of rigour and false assumptions in successional approaches to fungal ecology. In part these relate to insufficient consideration of the development of natural communities in relation to both time and space, as opposed to observations of purely temporal changes in floristic composition, sometimes based on the presence of reproductive structures as opposed to mycelia (Rayner & Todd, 1979; Cooke & Rayner, 1984). One particularly important consideration which is often neglected, is the fact that extension of indeterminate mycelial thalli is an integral part of community development. It is therefore always difficult to be certain of the time at which fungi first colonise a substratum, as opposed to when they become dominant.

Approaches to identification

Direct inoculation of natural or semi-natural substrata in the laboratory. This usually involves pairings of pure cultures of fungi in 'appropriate' substrata such as pine needles, leaf discs or wood-blocks. These are often sterilised to eliminate contaminants – the first stage of distancing from field conditions. Secondly, it is always difficult to maintain such natural substrata under appropriate micro-environmental conditions, especially with regard to moisture availability and aeration, so that although the methods are convenient, the results obtained are frequently disappointing adding little or nothing to those obtained from cultural experiments.

One unusual example of how this type of approach can be very effective, however, assesses the interactions of coprophilous fungi. Previously-sterilised food can be inoculated with spores of fungi prior to being fed to an animal, and the effects of interaction on fungal development within the dung then studied (Wicklow, 1981*b*).

Primary capture of a vacant resource. Another approach, applicable in the laboratory, is to expose a unit of uncolonised resource, such as a wheat straw or leaf disc, to a natural or semi-natural inoculum such as unsterile soil, or soil sterilised and inoculated with several different fungi. This type of approach formed the basis of the 'Cambridge'

method, used by Garrett to study competitive saprophytic colonisation referred to previously, and more recently, has been adapted by Fisher (1977, 1979) in a study of aero-aquatic hyphomycetes.

As already emphasised, this type of approach really takes into account only competition for primary resource capture, unless the experiment is maintained over a prolonged period. The difficulties of maintaining conditions appropriate to those of the field, mentioned for direct inoculation, may still apply. Furthermore, the approach may not be consistent with natural patterns of colonisation, in that sudden exposure of a vacant resource unit is possibly a rare phenomenon in nature. It is therefore likely to give undue prominence to fungi with ruderal characteristics.

Direct inoculation into substrata in the field. This approach obviates the difficulties of maintaining appropriate environmental conditions and has proved useful, for example, in elucidating the interactions that occur between bark-inhabiting fungi (Webber, 1979; Lonsdale & Sherriff, 1983). In such a study, Webber (1979) inoculated a variety of elm bark saprotrophs into uncolonised inner bark (phloem) and into already-colonised inner bark of recently cut elm logs which were left in the field. By later estimating the extent of colonisation by fungi introduced into the fresh bark, as opposed to the extent of colonisation by fungi introduced into already-occupied bark, it was possible to assess which of the saprotrophs tended to be effective in primary resource capture and which in secondary resource capture respectively.

However, using such methods the timing of inoculation may be inappropriate in relation to the natural processes of community establishment and development, or inocula may be unrepresentative of the natural methods of arrival and establishment. The latter problem was encountered in the study of elm bark saprotrophs already mentioned. One particular species, *Phomopsis oblonga* only colonised inner bark extensively when inoculated in the form of a precolonised bark plug, failing to do so when introduced as a spore suspension. Later observations have suggested that inner-bark colonisation by this fungus would not normally occur from a spore inoculum as it apparently exists in a mycelial form in the outer bark of healthy elms, and invades the inner bark from this inoculum source with the onset of the tree's death (Webber & Gibbs, 1983).

Following processes of natural community development. Ultimately, the approach most likely to provide us with an understanding of mycelial

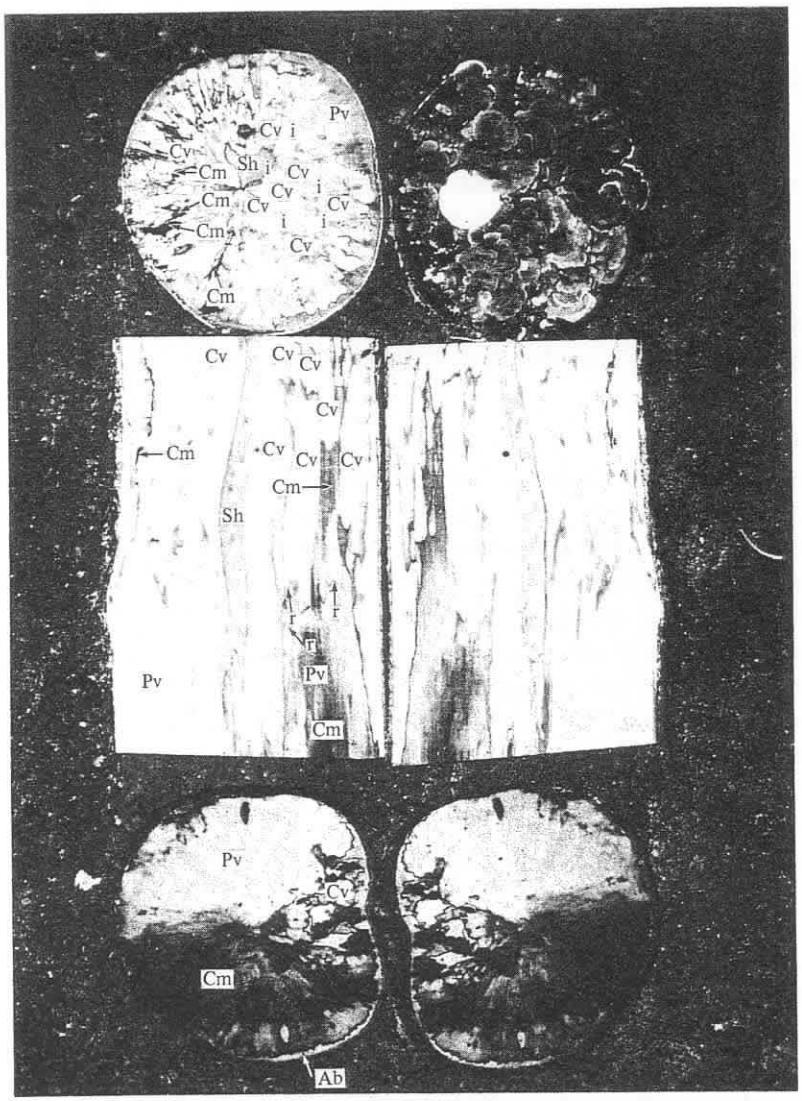

Fig. 10. Community organisation in a beech log which had been placed upright with its base buried in soil and litter two years previously at a deciduous woodland site. The log has been cut transversely near the top and bottom surfaces, and longitudinally for the intervening length, so that the three-dimensional distribution of columns of decay and discolouration can be ascertained. The upper surface is covered by basidiocarps of *Coriolus versicolor*. The distribution of some of the fungi present is indicated by the following symbols: Ab, *Armillaria bulbosa*; Cm, *Chaetosphaeria myriocarpa* (conidial stage) occupying interaction zones and other regions not occupied by active decay fungi;

interactions as they occur in nature, is to study them within the context of natural colonisation processes. However, this demands that sufficient account be taken of spatio-temporal characteristics of mycelia, and, as already indicated this has not always been a feature of succession studies. In turn, this requirement means that spatially defined resource units are the most suitable for study, and that analysis of interactions involves necessarily destructive methods. Wood represents such a spatially defined resource, and the ease with which populations and communities of mycelial individuals within it can be observed and their distribution mapped by direct methods makes it arguably the best example of the successful application of this approach. However, this should not be taken to imply that the approach is unlikely to be successful in other, perhaps less bulky substrata, although the techniques required to study mycelial distribution on a micro- rather than a macro-scale may need to be more sophisticated in these venues (Frankland, 1981). As a general principle, as the size of a resource unit is reduced, so the available surface for its colonisation, in relation to volume, increases proportionately. The result is that similar numbers of mycelial individuals may often be present in substrata of markedly different sizes (Cooke & Rayner, 1984; Boddy: Chapter 12; Rayner *et al.*: Chapter 23).

Two approaches are available for the study of natural colonisation processes in defined resource units. In the first, the community patterns present in a resource unit at any one time may be analysed, from which the events that have given rise to that pattern may be extrapolated. Comparison of such resource units at various stages of colonisation may provide further, indirect evidence of community development processes, but doubt must always remain concerning the inevitably speculative conclusions drawn. In wood, it is often quite easy, by analysis of the community pattern at any one time, to infer interaction patterns. For example, the presence of zone lines between different individuals, or of a series of relict zone lines left behind by a retreating individual can provide direct evidence of deadlock and replacement interactions respectively (Rayner & Todd, 1979; Fig. 10). As an example of the

Caption for Fig. 10 (*cont.*)

Cv, *Coriolus versicolor* individuals; Pv, *Phanerochaete velutina* invading from the base; Sh, *Stereum hirsutum*. i, interaction zone lines between individuals of the same and different species; r, relic zone lines left behind during replacement by *P. velutina*. (After Coates, 1984.)

potential usefulness of this approach, Boddy & Rayner (1983*b*) have recently applied it in a study of colonised attached oak branches, and been able to draw conclusions concerning the ecological roles of twelve different Basidiomycotina involved.

The other approach which allows more certainty about sequential processes, is simultaneously to expose large numbers of resource units to colonisation, then to sample these over a period of time and to analyse the community patterns at each sampling. Figure 11 illustrates community development processes observed in partly buried cut beech logs during such an experiment. The main disadvantage of this approach is the same as that described with the 'Cambridge' method; that it may not reflect the natural colonisation processes where large volumes of colonisable resource are not typically made suddenly available in this way.

Interactions and predictive ecology

In examining the role of mycelial interactions in natural community development processes, two issues are paramount. One con-

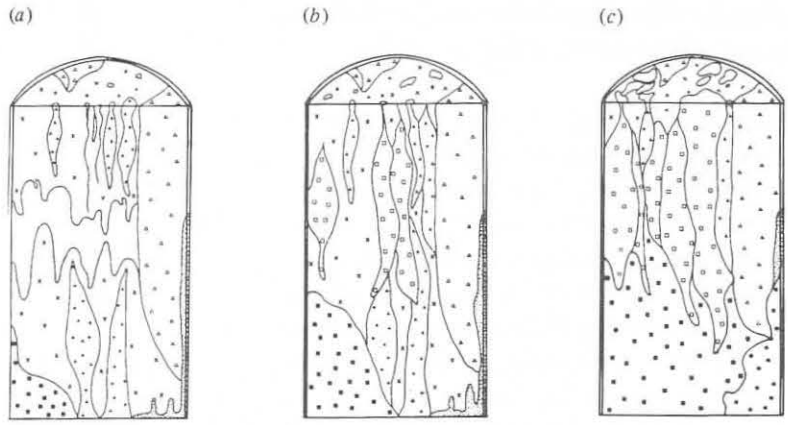

Fig. 11. (a–c). Idealised diagrams illustrating a typical pattern of decay community development in a cut beech log from the same experiment as that shown in Fig. 10. The community patterns at 6, 12 and 18 months respectively are shown. x, stained or discoloured wood containing microfungi and/or the Basidiomycotina *Chondrostereum purpureum* and *Corticium evolvens*; ▲, *Xylaria hypoxylon*; △, *Hypoxylon nummularium*; □, combative air-borne Basidiomycotina, e.g. *Coriolus versicolor, Bjerkandera adusta* and *Stereum hirsutum*; ■, combative early-arriving cord-formers, e.g. *Phallus impudicus* and *Tricholomopsis platyphylla*; ●, combative late-arriving cord-formers, e.g. *Phanerochaete velutina*; stipple, *Armillaria bulbosa*. (From Coates, 1984.)

cerns the extent to which events occurring under laboratory conditions are likely to change under different circumstances. Related to this, there is the need to consider the particular circumstances under which fungal colonisation occurs in nature, and hence the extent to which mycelial interactions are likely to be crucial determinants of the process.

Relationship between laboratory and field events

The most obvious way of ascertaining the relationship between laboratory and field events is to compare them directly and determine whether they are essentially the same, or, if they differ, in what ways. Such comparisons may ultimately yield understanding of which types of interactions observed in culture are likely to be repeated in nature.

Observations with wood decay fungi suggest that interactions observed under cultural conditions favouring dense mycelial growth (as on 2–3% malt agar) and mediated via hyphal or mycelial contact mechanisms will be broadly similar to those in naturally decomposing wood. Furthermore, there is evidence of strong correlation between the combative ability of these fungi in culture and their ecological roles (Rypacek, 1966; Henningson, 1967; Rayner, 1978; Thompson, 1982; Boddy & Rayner, 1983a,b; Coates, 1983). Primary colonisers of standing or recently felled trees are typically non-combative, being readily replaced. These include true heartrot fungi such as *Laetiporus sulphureus* and *Rigidoporus ulmarius*, together with species colonising recently functional sapwood, such as *Chondrostereum purpureum, Corticium evolvens, Flammulina velutipes* and *Peniophora quercina.* Airborne colonists of exposed non-living woody surfaces, such as the ubiquitous *Coriolus versicolor* and *Stereum hirsutum* are capable of replacement of pioneers, and of deadlock against one another. Mycelial cord-forming species, such as *Tricholomopsis platyphylla, Phallus impudicus, Phanerochaete velutina* and *Hypholoma fasciculare* invading from the soil and litter are highly combative, readily replacing many other species, in spite of their typically moderate or slow mycelial extension rates in culture. This corresponds with the fact that many seem to become established in wood via secondary resource capture. The closely related species pair, *Phlebia radiata* and *Phlebia rufa* provide further demonstration of the principles. *P. rufa* appears to be a pioneer invader of attached, light-suppressed branches and trunks especially of oak (*Quercus* species), whilst *P. radiata* is a ubiquitous invader of felled, fallen or already decomposing deciduous timber. *P.*

rufa is less combative, and fruits more readily in culture than *P. radiata* (Boddy & Rayner, 1983*a*).

These examples should not be taken to imply that Basidiomycotina are the only fungi in which a combative hierarchy may be present. Certain Deuteromycotina and Ascomycotina such as *Trichoderma* and *Scytalidium* species show a strong capacity to replace even some of the most combative wood-decaying fungi such as *Phanerochaete velutina.* These non-Basidiomycotina appear to have an essentially scavenging role in nature, and often develop in wood which has undergone decomposition or been subjected to disturbance. Their combative characteristics may assist establishment at later stages of community development, but much interest has also been raised by the possibility of introducing them directly into undecayed wood as biological control agents of decay (Hulme & Shields, 1972). Furthermore, in locations where Basidiomycotina do not readily become established, as in bark, similar patterns of behaviour may occur amongst other fungi.

These observations apply to fungal colonisation of essentially uncomminuted resources, that is before they become subject to extensive invasion by fauna. It is in such resources that purely mycelial interactions are likely to play a significant rôle in community development processes. Within these terms, the emphasis on soil as a habitat in early studies of fungal interactions, with its focus on antibiosis as a major mechanism of antagonism, is seen as being somewhat unfortunate. Very probably, the essential life styles of many soil fungi consists of long periods of inactivity under starvation conditions, alternating with sudden bursts of activity associated with localised nutrient enrichment, as from root exudates. Such fungi would be expected to have predominantly stress-tolerant ruderal characteristics, with an absence of combative mechanisms. However it may be that in comminuted resources such as soil (where diffusion is facilitated), antagonistic action in the form of antibiosis can be effective, although it has only occasionally been possible to prove that these substances are produced *in vivo*. The *Trichoderma* effect outlined earlier, is one such example of diffusible antibiosis that apparently occurs in soil at root surfaces (Brasier, 1978). Animal invasion of woody substrata with accompanying comminution, which introduces a major destabilising influence via direct effects both on fungi and on the resource (Anderson, Rayner & Walton, 1983), may also allow antibiotic producing fungi to exert a significant effect under natural conditions.

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Interactions and community development patterns

It will now be evident that the significance of any interaction will need to be qualified by the circumstances under which fungal development takes place. In addition, the stage at which colonisation occurs will be an important determinant of the actual contribution (if any), which interactions make to community processes. For example, the conditions under which colonisation is initiated may be sufficiently selective, that is impose sufficient stress, to exclude all but one or a few fungi with consequent reduction in the number of potential interactions. Also, during early stages of colonisation, whilst the community is still 'open', the emphasis will be on primary resource capture, whilst at later stages, as the community 'closes', combative interactions are likely to assume increasing importance.

In this context, there is a need to understand the range of pathways along which natural community development may flow. Cooke & Rayner (1984) have attempted to provide a framework for such an understanding, and this is illustrated by the schema in Fig. 12. They suppose that colonisation processes may be initiated under two distinctive circumstances, either under conditions of some form of stress (probably the predominant circumstance in nature) or in the relative absence of such conditions (predominant in many 'experimental' successions). Hereafter, the sequence of events is determined by stress-alleviation, such as humidification of orginally relatively dry material as a result of metabolic activity, or stress-aggravation, involving imposition of new or additional stress, such as elevation of temperature also due to metabolic activity, and disturbance through the provision of new colonisable substrata by partial or total destruction of the resident biomass, or enrichment with additional resources.

Practical exploitation. The most obvious practical outlet for interaction studies is in the development of effective biological control for use against a pathogen or 'pest' fungus. In addition, there is the general ecological need to understand the consequences of any form of interference with ecosystem functioning, and the probability of exploiting 'favourable' interactions in such processes as waste disposal and food production.

Two basic methods are available in relation to exploitation of fungal interactions. The first is directly to introduce the favoured organism(s) into the system. The second is by manipulation of environmental conditions to alter the balance in favour of selected organisms. In all

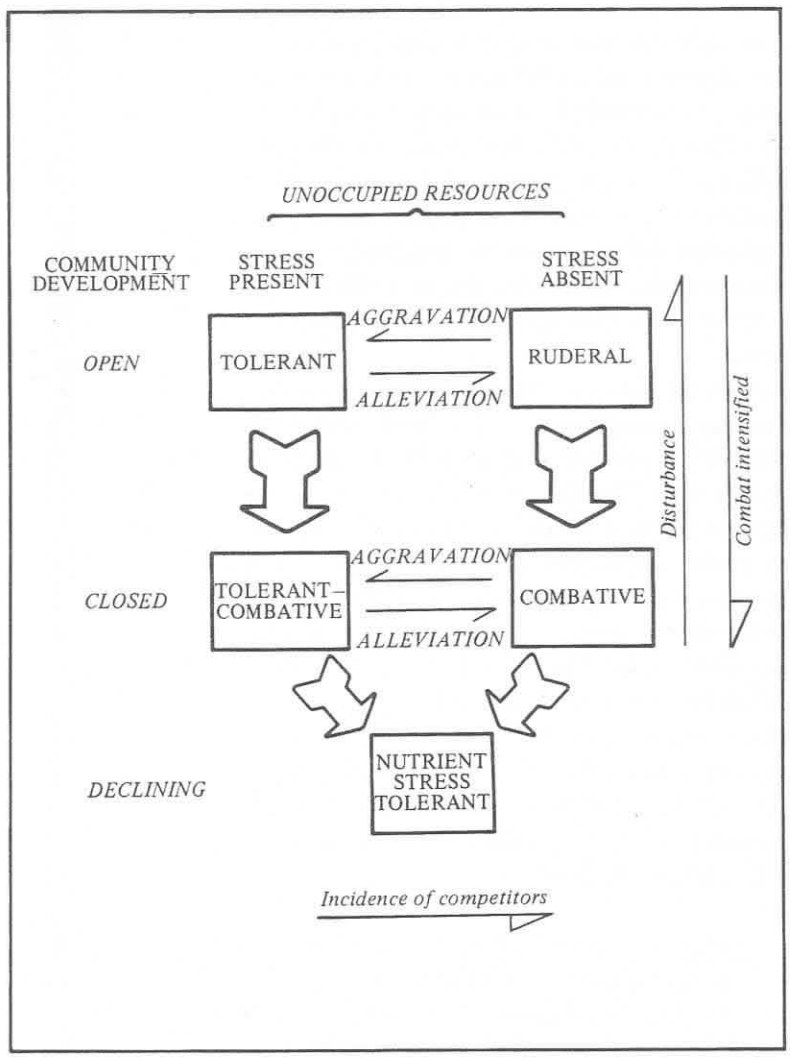

Fig. 12. Diagram of possible community development pathways from colonisation of a totally unoccupied resource, through an open community stage with still unoccupied resources available for primary capture, to a closed community with all initial primary capture completed. Culmination is a declining community stage characterised by severe nutrient stress. In the absence of competitors, developing tolerant communities may progress directly to declining tolerant communities without an intermediate combative stage. (Simplified from Cooke & Rayner, 1984.)

cases the successful application of knowledge of interactions is dependent on understanding the circumstances under which they are likely to operate.

Thus in relation to biological control there is little to be gained from attempting to introduce a suitable agent into a system in which the conditions do not favour establishment. Related to this, the principles underlying preventative as opposed to curative biological control measures are likely to be fundamentally different, in that preventative measures will usually involve primary resource capture competition, whilst curative measures are likely to involve secondary resource capture or direct parasitism. Adhering to the principle that prevention is better than cure, first considerations should be paid to abilities of a potential control agent in primary capture. From this point of view, its interaction performance in culture may be a secondary consideration, as selection of potentially useful agents should not necessarily be based on observations of replacement or antibiotic reactions. It is only necessary for the biotic agent to prevent establishment of the target organism, not to replace or kill the latter. Furthermore, since community development processes have been initiated in the absence of the target organism, it is unlikely to establish at a later stage even if the primary control agents are themselves subsequently replaced. In part, this statement reflects the fact that many pest fungi are by their very nature, primary colonisers.

It follows from this that a useful first approach to investigating possibilities of biological control is to study processes of primary capture. Thence a selected species may be given an advantage in primary capture, via direct inoculation and/or manipulation of conditions, which deflect community establishment processes away from the target organism. Consciously or subconciously, this approach has underlain several examples of biological control. Thus direct inoculation of *Phlebia gigantea* to freshly cut conifer stumps has been widely used to prevent establishment of *Heterobasidion annosum*. The essential feature here is that *P. gigantea* was initially selected as a primary coloniser of stump surfaces, rather than a direct 'antagonist' of *H. annosum*. Following inoculation there is extensive primary capture by *P. gigantea* which limits establishment of *H. annosum*, perhaps partly associated with hyphal interference mechanisms which prevent replacement by the latter (Rishbeth, 1963; Ikediugwu *et al.*, 1970). Another similar example is the treatment of pruning wounds on plum trees with *Trichoderma viride*, which prevents the establishment of

Chondrostereum purpureum (Grosclaude, Ricard & Dubos, 1973). A classical indirect mechanism is the ring barking of tropical trees prior to felling and establishment of tea plantations, which reduces problems associated with *Armillaria* due to shift towards other root-colonising fungi in treated trees (Leach, 1937). Similarly ammonium sulphamate treatment of hardwood stumps may favour root colonisation by fungi other than *Armillaria* species (Rayner, 1975, 1977).

Within the context of biological control via exploitation of primary resource capture, the emphasis is on the manipulation of an endogenous community to alter the balance away from a target organism. Nonetheless, it has sometimes been suggested that a successful biological control agent is unlikely to be found within an existing system where the target organism is already in balance with its potential competitors, and hence that emphasis should be on the introduction of exotic agents (Baker & Cook, 1974). This is clearly inappropriate for primary capture mechanisms of control, but may be more pertinent when considering curative measures employing secondary resource capture or parasitism. Whilst applicable in certain instances of control of animal pests, it remains to be seen whether this has application to fungi. In all events establishment under the prevailing natural conditions remains of overriding importance.

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